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Plant and vegetation functional responses to cumulative high nitrogen deposition in rear-edge heathlands

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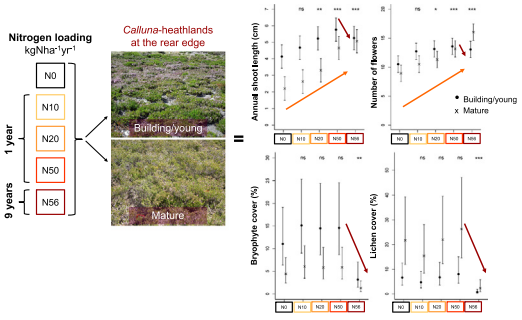
HIGHLIGHTS

- The annual growth and flowering of *Calluna* plants responded positively to N addition.
- Young plants showed early signs of N saturation under cumulative (9-year) N loading.
- There were no significant N-driven changes in plant species composition and richness.
- Mosses and lichens cover declined only with cumulative N at both young/mature heaths.
- Marginal *Calluna*-heathlands are thus moderately resistant to cumulative high-N inputs.

GRAPHICAL ABSTRACT



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ABSTRACT

Elevated atmospheric nitrogen (N) deposition is a major driver of change, altering the structure/functioning of nutrient-poor *Calluna vulgaris*-heathlands over Europe. These effects amply proven for north-western/central heathlands may, however, vary across the ecosystem's distribution, especially at the range limits, as heathlands are highly vulnerable to land-use changes combined with present climate change. This is an often overlooked and greatly understudied aspect of the ecology of heathlands facing global change. We investigated the effects of five N-fertilisation treatments simulating a range of N deposition rates (0, 10, 20, and 50 kg N ha^{-1} yr^{-1} for 1 year; and 56 kg N ha^{-1} yr^{-1} for 9 years) on the *Calluna*-plants, the plant functional groups, species composition and richness of two life-cycle stages (building/young- and mature-phase) of *Calluna*-heathlands at their rear-edge limit. Our findings revealed a dose-related response of the shoot length and number of flowers of young and mature *Calluna*-plants to the addition of N, adhering to the findings from other heathland locations. However, cumulative high-N loading reduced the annual growth and flowering of young plants, showing early signs of N saturation. The different plant functional groups showed contrasting responses to the cumulative addition of N: annual/perennial forbs and annual graminoids increased with quite low values; perennial graminoids were rather abundant in young heathlands but only slightly augmented in mature ones; while bryophytes and lichens strongly declined at the two heathland life-cycle stages. Meanwhile there were no significant N-driven changes in plant species composition and richness. Our results demonstrated that *Calluna*-heathlands at their low-latitude distribution limit are moderately resistant to cumulative high-N loading. As north-western/central European heathlands under high-N inputs broadly experienced the loss of plant diversity and pronounced changes in plant species dominance, rear-edge locations may be of critical importance to unravel the mechanisms of heathland resilience to future global change.

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1. Introduction

Human activities have exceedingly increased the mobility and deposition of biologically reactive forms of nitrogen (N) in recent decades worldwide (Galloway et al., 2004, 2008; Peñuelas et al., 2017). This anthropogenic disruption of the global N cycle is responsible for biodiversity loss and altered ecosystem processes in a great variety of terrestrial ecosystems (e.g., Bobbink et al., 2010; Ochoa-Hueso et al., 2011). What is more, cumulative N inputs are one of the most significant factors producing unprecedented changes in the functioning of ecosystems, even at low deposition rates (Clark and Tilman, 2008; De Schrijver et al., 2011; Humbert et al., 2016; Phoenix et al., 2012). Understanding the magnitude of the effects of long-term airborne N depositions is, therefore, of major importance for the preservation of ecosystems, in particular, semi-natural habitats adapted to low levels of N availability (Field et al., 2014; Humbert et al., 2016; Phoenix et al., 2012; Soons et al., 2017; Stevens et al., 2016).

Heathlands dominated by the dwarf shrub *Calluna vulgaris* (L.) Hull (henceforth referred to as *Calluna*) are semi-natural ecosystems on nutrient-poor soils pertaining to traditional cultural landscapes within Atlantic Europe (Loidi et al., 2010), highly endangered across their entire distribution range (Fagúndez, 2013). Land-use changes (abandonment or intensification), N pollution, natural succession, and invasion by exotic species are the main drivers causing heathland habitat destruction and fragmentation throughout Europe (e.g., Bartolomé et al., 2005; Britton et al., 2017; Henning et al., 2017; Rose et al., 2000). Many heathland field-surveys and N-manipulation experiments over different temporal scales have strongly demonstrated that elevated N deposition leads to (1) changes in plant growth, phenology and chemistry (e.g., Bähring et al., 2017; Britton and Fisher, 2008), (2) increased plant sensitivity to abiotic/biotic stressors (e.g., Heil and Diemont, 1983; Prins et al., 1991), (3) a reduction in plant diversity (Britton and Fisher, 2007; Maskell et al., 2010; Southon et al., 2013), (4) the loss of N-sensitive plant species (Caporn et al., 2014; Van den Berg et al., 2008), and (5) the invasion by nitrophilous species (Britton and Fisher, 2007; Southon et al., 2013). Moreover, a few long-term researches demonstrated the lasting nature of the majority of these N-driven impacts on the heathland ecosystem (Carroll et al., 1999; Field et al., 2017; Power et al., 2006; Southon et al., 2012) that are expected to continue over coming decades (Payne et al., 2017; Stevens et al., 2016). These studies, however, have principally been accomplished in north-western and central European *Calluna*-heathlands; very little is known about the responses of southern heathlands at the rear-edge of the ecosystem's distribution to elevated N availability (Calvo et al., 2005, 2007; Cuesta et al., 2008; Marcos et al., 2003), especially over the long-term (Calvo-Fernández et al., 2018; Taboada et al., 2016). This lack of knowledge impedes the implementation of proper on-site management to counterbalance the potentially detrimental impacts of N loading in rear-edge heathland locations that are also vulnerable to present climate change (Fagúndez, 2013). Whereas for other heathland areas across Europe, diverse management measures (e.g., grazing, mowing, prescribed burning, sod-cutting; Härdtle et al., 2009; von Oheimb et al., 2009) have been tested for their effectiveness in maintaining the low-nutrient status of the given heathland location with minor adverse impacts on the ecosystem (see review by Jones et al., 2017).

Recent researches have shown that environmental factors affect species differentially at the centre and the edges of their distribution ranges (e.g., Pearson et al., 2009; Viejo et al., 2011; see review by Sagarin et al., 2006), with notable dissimilarities between leading and rear edges (i.e., high- and low-latitude limits, respectively; Hampe and Petit, 2005). This generally implies that findings from a given location within a species' range might not be applicable to other parts of the range (Sagarin et al., 2006). Within the broad distribution area of *Calluna*-heathlands across Europe, it is very likely that dominant *Calluna* plants from different locations have evolved particular adaptive traits to their local conditions (Loidi et al., 2010) and are, thus, differentially sensitive to environmental changes. To our knowledge, though, only one study (Meyer-Grünefeldt et al., 2016) has experimentally assessed how central and marginal *Calluna* plants responded to global change testing the single and combined effects of drought and N deposition. This study concluded that (1–2-year-old) plants from the southern-most limit of the *Calluna*-heathland ecosystem's distribution are better adapted to drought events than those from the centre of the range, except under elevated N availability. It is, however, difficult to extrapolate the results of these short-term effects on potted *Calluna* seedlings to long-term effects on more complex natural systems. Further research is, therefore, necessary to investigate the differential resistance of *Calluna*-heathlands across the entire distribution range to shifting environments under global change.

Here, we evaluate the impact of different doses of N loading (0, 10, 20, and 50 kg N ha^{-1} yr^{-1} for 1 year, and 56 kg N ha^{-1} yr^{-1} for 9 years) on the functioning of *Calluna*-heathlands at their southern-most distribution limit by assessing the responses of two life-cycle stages of *Calluna*-heathland development: building/young (9-year-old plants) and mature (30–40-year-old) growth phases (Gimingham, 1972). To date, there are only a few studies testing how age affects heathland responses to N deposition (Caporn et al., 2014; Jones and Power, 2015; Meyer-Grünefeldt et al., 2015, 2016); this is despite contrasting plant growth rates and vegetation structures among heathland life-cycle stages (i.e., pioneer, building, mature and degenerate phases; Gimingham, 1972). Specifically, we examine how increased N inputs alter the annual growth and flowering of *Calluna*, the different plant functional groups (annual/perennial forbs and graminoids, woody species, bryophytes and lichens), and plant species composition and richness. According to prior findings from north-western and central European heathlands, we hypothesised that experimentally-increased N availability in rear-edge heathlands will result in: (i) enhanced *Calluna*-plant productivity (Bähring et al., 2017; Britton and Fisher, 2008; Southon et al., 2012) especially at the building stage due to higher plant growth rates and nutrient demand (Jones and Power, 2015); (ii) a shift in plant species composition towards more nitrophilous plant communities (Britton and Fisher, 2007; Southon et al., 2013) with higher relative abundances of graminoid species (Bobbink and Heil, 1993; Friedrich et al., 2011; Prins et al., 1991); and (iii) a decline in plant species richness (Maskell et al., 2010; Southon et al., 2013) associated to the loss of N-sensitive species (Caporn et al., 2014; Van den Berg et al., 2008) such as bryophytes and lichens (Bähring et al., 2017; Pilkington et al., 2007), particularly with cumulative (9-year) N inputs (De Schrijver et al., 2011).

2. Material and methods

2.1. Study area

The study was conducted in three *Calluna* heathland sites (San Isidro, Riopinos I, and Riopinos II) located in the Cantabrian Mountains (NW Spain; 43°02–03′N, 5°21–26′W; 1560–1660 m a.s.l.; 18–35 ha in size) [see Calvo-Fernández et al., 2018 for additional information] included as priority habitat type in Annex I of the Habitats Directive (92/43/ECC; habitat code 4060: alpine and boreal heaths). The climate is Eurosiberian (total precipitation of 1308 mm and mean temperature of 7.0 ± 4.9 °C during the study year 2014) with a brief and moderate drought period in July–August, and a snow cover duration from late-autumn until the end of May. Soils are Umbrisol characterised by high acidity (pH = 3.9 ± 0.14; deionized water), low fertility, sandy texture and high permeability (Marcos et al., 2009). The vegetation growing season comprises from May to October and the bud burst of *Calluna* plants happens in June. The three sites are subjected to minimal regular free-range grazing by cattle and horses (1–2 LU ha^{-1} yr^{-1}) in June–September. Total N deposition in the study area ranges from 7.5 to 15 kg N ha^{-1} yr^{-1}, according to the EMEP and CHIMERE models for

Spain (García-Gómez et al., 2014), while bulk inorganic N deposition for the period 2011–2014 was 4.6 kg N ha^{-1} yr^{-1} (Calvo-Fernández et al., 2017). Therefore, total N deposition in the study area is either lower than or within the critical load range estimated to threaten the persistence of European dry *Calluna*-heathlands (i.e., 10–20 kg N ha^{-1} yr^{-1}; Bobbink et al., 2010; Hall et al., 2015).

2.2. Experimental design

In each study site, we selected two heathland life-cycle stages: (1) young stands rejuvenated by prescribed fire in 2005, i.e., 9 years old at the time of the vegetation survey (building-phase; Gimingham, 1972), and (2) mature stands showing the first signs of degeneration after 30–40 years of land use abandonment (mature-phase; Gimingham, 1972). After perturbation, *Calluna* plants in the study area regenerate slowly and predominantly from seed germination and, to a much lesser extent, by vegetative resprouting (Calvo et al., 2002; Valbuena et al., 2000). We established a total of 90 2 m × 2 m plots and performed a manipulative experiment consisting of five randomly-assigned N-fertilisation treatments (i.e., 3 replicated plots per N treatment, age class, and site) in addition to background atmospheric N deposition. The yearly amount of added N in each treatment was: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) of solid granules of ammonium nitrate, monthly added by hand to the soil surface in June–November 2013 and 2014 (6 times in 2013, and before vegetation sampling in 2014) (short-term: 1 year); and 56 kg N ha^{-1} yr^{-1} (N56) monthly added in May–October from 2005 to 2014 (6 times per year from 2005 to 2013, and before vegetation sampling in 2014) (long-term: 9 years). The N56 treatment corresponded to ca. two times the maximum total N deposition levels in the study area at the beginning of the experiment (Rivero Fernández et al., 1996) and was equivalent to the highest predicted N input by 2050 for southern Europe (Galloway et al., 2004).

2.3. Vegetation survey

To evaluate the effects of the different N-fertilisation treatments on the annual growth and flowering of *Calluna* plants, in each plot we measured the length and counted the number of flowers of five randomly-selected *Calluna* apical shoots of the current year in July 2014.

We also investigated the functional responses of the heathland vegetation to N fertilisation by determining the percentage cover of the different plant functional groups, the plant species composition, and the total number of plant species (species richness) in each plot in July 2014. To do this, we estimated the percentage cover of all vascular and non-vascular plant species in four 1 m × 1 m quadrats in each 2 m × 2 m plot, and calculated the mean percentage cover of the following plant functional groups: perennial forbs, annual forbs, perennial graminoids, annual graminoids, woody species, bryophytes, and lichens.

2.4. Data analysis

We fitted linear mixed models (LMMs) to test the effects of heathland age and N fertilisation on the annual growth and flowering of *Calluna* plants. The response variables in the models were mean annual *Calluna* shoot length and number of flowers. We modelled the response variables assuming a Gaussian error distribution, using the identity link function. The predictor variables (fixed factors) were the age of *Calluna* plants (young and mature), the N treatment (N0, N10, N20, N50, and N56), and their interaction. Minimal adequate models (MAMs) to describe the data were determined by the Akaike's information criterion (AIC) by means of the "anova ()" function. Also, we initially used the AIC to compare (a) the fit of LMMs with the identity of the sampling plots nested within each heathland site as a random factor, (b) the fit of LMMs with the identity of the heathland sites as a random factor, and (c) the fit of generalised least squares (GLS) models without the random factor, using restricted maximum likelihood estimation (REML) procedures, by means of the "anova()" and "gls()" functions. Models with the identity of the heathland sites as a random factor were the most parsimonious ones, and, therefore, the ones that are reported.

We evaluated the effects of heathland age and N fertilisation on total plant species richness by performing a generalised linear mixed model (GLMM) with the total number of species as the response variable, modelled following a Poisson error distribution (log link function). We also fitted analogous GLMMs with the percentage cover of the different plant functional groups: (1) perennial forbs, (2) annual forbs, (3) perennial graminoids, (4) annual graminoids, (5) woody species, (6) bryophytes, and (7) lichens, as the response variables modelled following a quasi-Poisson error distribution (log link function) to account for overdispersion. The predictor variables (fixed factors) were the age of *Calluna* plants, the N treatment, and their interaction. The interaction term was retained in the models only when significant. The identity of the sampling plots nested within each heathland site was included in the models as random factor and retained only when accounted for >5% of the variation.

We obtained predicted values of all the response variables in the models (except for annual forbs and annual graminoids due to very low percentage cover values) for each *Calluna* age and N treatment, without taking the uncertainty of the random effects parameters into account, and computed 95% confidence intervals based on a normal approximation. Significance levels of the difference between each N-fertilisation treatment (N10, N20, N50, and N56) and the control treatment (N0), obtained directly from the model summary outputs, are indicated in the figures.

Differences in plant species composition among N treatments and heathland ages were tested with non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (MANOVA) [999 permutations; sequential sums-of-squares (type I)] using community distance matrices and the "metaMDS()" and "adonis2()" functions. We used the Bray-Curtis dissimilarity index to calculate the site x species distance matrix, and evaluated the quality of the ordination with the stress value (i.e., the mismatch between distance measures and distances in the ordination space). Only species present in at least 20% of the sampling plots (i.e., 6 plots, 19 species) were included in the ordination. Predictors were the age of *Calluna* plants, the N treatment, and their interaction.

All data analyses were carried out with R software, version 3.3.1 (R Core Team, 2016) using the "stats", "MASS" (Venables and Ripley, 2002), "nlme" (Pinheiro et al., 2016), and "vegan" (Oksanen et al., 2017) packages.

3. Results

3.1. Calluna shoot length and flowering

The annual growth and the number of flowers of the apical shoots of both young and mature *Calluna* plants responded positively to the experimental increase in N availability (i.e., positive dose-related responses), and were significantly higher at the N20, N50, and N56 treatments compared to the control (Fig. 1, Table 1). However, we found opposite responses of annual growth and flowering to the cumulative (9-year) addition of N (N56 treatment) for each life-cycle stage of the *Calluna* plants (significant 'age x N treatment' interaction terms). Relative to the rest of the N-fertilisation treatments, the shoot length and flowering values at the N56 treatment progressively increased for mature plants, while they both decreased in case of the young ones. Moreover, young *Calluna* plants at the building stage generally exhibited greater annual shoot length values than mature ones.

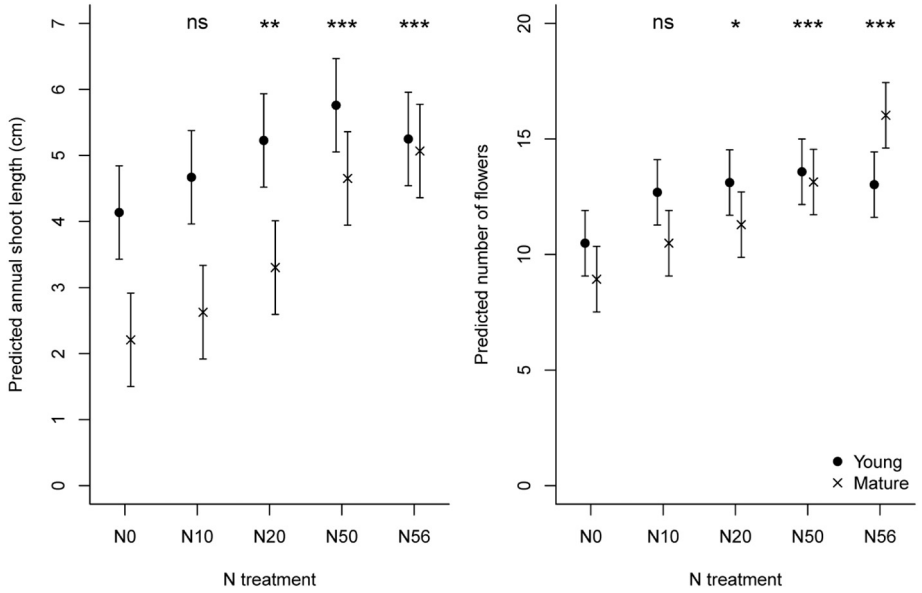

Fig. 1. Model predicted values (mean ± 95% confidence intervals) of annual shoot length (cm) and number of flowers of *Calluna* plants in the two differently aged heathland areas [young (black filled circle), mature (cross)] and the five N treatments: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) for 1 year (short-term); and 56 kg N ha^{-1} yr^{-1} (N56) for 9 years (long-term). Significance levels of N treatments with respect to the control treatment (N0) are indicated by *** ($0.001 > p$), ** ($0.01 > p > 0.001$), * ($0.05 > p > 0.01$), and ns ($p > 0.05$).

3.2. Plant functional groups and species composition

The majority of plant functional groups responded statistically significantly to the experimental increase in N loading, especially to the cumulative (9-year) input of N (N56 treatment), and similarly for the two heathland ages (non-significant 'age x N treatment' interaction terms) (Table 2).

The percentage cover of perennial forbs and perennial graminoids increased significantly at the N56 treatment compared to the control, for both heathland ages in case of perennial forbs, but only at mature heathlands in case of perennial graminoids (Fig. 2, Table 2). Moreover, we found significantly higher values of perennial forbs at the N10 treatment relative to the control. In general, perennial forbs exhibited low percentage cover values (young heathlands: mean ± standard deviation = 1.7 ± 2.2; mature heathlands: 0.8 ± 2.0); meanwhile perennial graminoids were comparatively more abundant at young (25.4 ± 15.5) than at mature heathlands (3.9 ± 6.5). The identity of the sampling plots within each heathland site (random factor in the models) explained a high amount (>50%) of the variation in the percentage cover of perennial forbs, while a low amount (<10%) in case of perennial graminoids (Table 2).

The percentage cover of annual forbs and annual graminoids responded significantly positively to the N56 treatment (Table 2), but reached very low average values (a single species with <1% and 5%, respectively) for both heathland ages (Tables 3 and 4). The identity of the sampling plots within each heathland site (random factor in the models) explained a very high amount (100%) of the variation in the percentage cover of both annual forbs and annual graminoids (Table 2).

We found no significant differences in the percentage cover of woody species among the different N-fertilisation treatments (Fig. 2, Table 2); but woody species had significantly higher cover values at the mature heathlands compared to the young ones (Fig. 2, Tables 3 and 4).

Finally, bryophytes were significantly more abundant at young heathlands, whereas lichens at mature ones (Fig. 3, Tables 3 and 4). The percentage cover values of both non-vascular plant functional groups significantly decreased at the N56 treatment relative to the control for both heathland ages (Fig. 3, Table 2).

We found no differences in plant species composition among the N-fertilisation treatments, but we did find statistically significant differences between the two heathland ages (Fig. 4, Table 5). Young heathlands were characterised by high cover values of graminoid species such as *Aira caryophyllea* L., *Carex nigra* (L.) Reichard, *Carex pilulifera* L., *Deschampsia flexuosa* (L.) Trin., *Festuca rubra* L., *Juncus squarrosus* L., and *Nardus stricta* L., and bryophytes (Fig. 4, Table 3). Meanwhile mature heathlands were characterised by high cover values of woody

Table 1
Linear mixed model (LMM) results for the effects of heathland age (young, mature) and N treatment on *Calluna* annual shoot length (cm) and number of flowers. N treatments: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) for 1 year (short-term); and 56 kg N ha^{-1} yr^{-1} (N56) for 9 years (long-term). The interaction term ('age x N treatment') was retained in the models only when significant. Standard deviations (SD) and variance components (%) of the random effects (identity of the heathland sites) are given. Df = degrees of freedom. Significant *p*-values are in bold face.

	Fixed effects				Random effects		
Response variable	Predictor variable	Df	F value	*p* value	Variable	SD	Variance
Annual shoot length (cm)	(Intercept)	1	343.62	<**0.001**	Heathland site	0.370	30.40
	Age	1	64.81	<**0.001**	Residual	0.847	69.60
	N treatment	4	20.43	<**0.001**			
	Age:N treatment	4	3.96	**0.006**			
Number of flowers	(Intercept)	1	1542.47	<**0.001**	Heathland site	0.398	16.53
	Age	1	2.03	0.158	Residual	2.010	83.47
	N treatment	4	14.78	<**0.001**			
	Age:N treatment	4	5.00	**0.001**			

Table 2
Generalised linear mixed model (GLMM) results for the effects of heathland age (young, mature) and N treatment on the percentage cover (%) of the plant functional groups (perennial forbs, annual forbs, perennial graminoids, annual graminoids, woody species, bryophytes, and lichens) and the total number of plant species (species richness). N treatments: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) for 1 year (short-term); and 56 kg N ha^{-1} yr^{-1} (N56) for 9 years (long-term). The interaction term ('age x N treatment') was retained in the models only when significant. Standard deviations (SD) and variance components (%) of the random effects (identity of the sampling plots nested within each heathland site) are given. Df = degrees of freedom. Significant *p*-values are in bold face.

	Fixed effects				Random effects		
Response variable	Predictor variable	Df	F value	*p* value	Variable	SD	Variance
Vascular species							
Perennial forbs cover	(Intercept)	1	4.79	**0.031**	Heathland site	1.235	48.20
	Age	1	32.54	<**0.001**	Sampling plot	1.327	51.80
	N treatment	4	2.74	**0.034**	Residual	1.7×10^{-5}	6.8×10^{-4}
Annual forbs cover	(Intercept)	1	1447.77	<**0.001**	Heathland site	1.0×10^{-20}	0.00
	Age	1	11.77	**0.001**	Sampling plot	24.699	100.00
	N treatment	4	6.55	<**0.001**	Residual	3.2×10^{-22}	0.00
	Age:N treatment	4	3.21	**0.017**			
Perennial graminoids cover	(Intercept)	1	153.24	<**0.001**	Heathland site	0.384	15.43
	Age	1	60.40	<**0.001**	Sampling plot	0.198	7.95
	N treatment	4	2.70	**0.037**	Residual	1.909	76.62
	Age:N treatment	4	4.21	**0.004**			
Annual graminoids cover	(Intercept)	1	56,895.73	<**0.001**	Heathland site	1.1×10^{-36}	0.00
	Age	1	53,522.00	<**0.001**	Sampling plot	1.387	100.00
	N treatment	4	7912.08	<**0.001**	Residual	9.1×10^{-36}	0.00
	Age:N treatment	4	8180.93	<**0.001**			
Woody species cover	(Intercept)	1	5847.54	<**0.001**	Heathland site	0.096	6.53
	Age	1	62.82	<**0.001**	Residual	1.368	93.47
	N treatment	4	0.48	0.750			
Non-vascular species							
Bryophyte species cover	(Intercept)	1	105.80	<**0.001**	Heathland site	0.344	13.54
	Age	1	25.58	<**0.001**	Residual	2.197	86.46
	N treatment	4	4.68	**0.002**			
Lichen species cover	(Intercept)	1	103.69	<**0.001**	Heathland site	0.402	16.65
	Age	1	28.75	<**0.001**	Sampling plot	0.533	22.08
	N treatment	4	8.16	<**0.001**	Residual	1.479	61.27
Total number of species	(Intercept)	1	553.11	<**0.001**	Heathland site	0.148	16.53
	Age	1	48.42	<**0.001**	Residual	0.750	83.47
	N treatment	4	1.12	0.352			

species such as *Calluna*, *Erica tetralix* L., and *Vaccinium myrtillus* L., and lichens, mainly *Cetraria islandica* (L.) Ach. and *Cladonia* spp. P. Browne (Fig. 4, Table 4).

3.3. Plant species richness

There were no significant differences in plant species richness among the N-fertilisation treatments for both young and mature heathlands (Fig. 5, Table 2). Then again young heathlands held a significantly higher number of plant species than mature ones.

4. Discussion

4.1. Dose-related responses of Calluna plants

The experimentally increased availability of N in the studied rear-edge *Calluna*-heathlands led to consistent dose-related responses of the annual growth and flowering of *Calluna* plants at both young and mature life-cycle stages. For the most part, the length as well as the number of flowers of the apical shoots of *Calluna* was significantly favoured by N fertilisation, except for young plants under cumulative (9-year) high-N (56 kg N ha^{-1} yr^{-1} plus background deposition) loading.

Firstly, these results reflect the findings of prior studies from north-western and central European heathlands (e.g., Bähring et al., 2017; Britton and Fisher, 2008; Southon et al., 2012; von Oheimb et al., 2010) and, thus, strongly suggest that the productivity of *Calluna* is primarily N-limited across the entire distribution range of *Calluna*-heathlands. However, the reported apparently positive impact of increasing N availability on the plant's performance requires careful consideration, because:

(1) N-driven increments in the annual growth of *Calluna* may entail greater plant susceptibility to a myriad of stress factors, including frost, drought (Meyer-Grünefeldt et al., 2016), and insect pests (Taboada et al., 2016). Nevertheless, no extensive *Calluna* plant mortality, dieback or severe damage have been detected since the beginning of the experiment in these montane heathlands (personal observations; see Calvo-Fernández et al., 2018), neither related to the cumulative loading of N nor caused by abiotic or biotic extreme events; oppositely to the findings reported from northern heathlands (Bjerke et al., 2017; Britton and Fisher, 2007; Carroll et al., 1999; Lee and Caporn, 1998; Log et al., 2017); and

(2) N-driven intensification of *Calluna* flowering may be ineffective in promoting plant reproduction and heathland regeneration, as either (i) the delay in seed germination (Valbuena et al., 2000) and the intense plant competition due to grass proliferation in young stands (Friedrich et al., 2011; Heil and Bruggink, 1987) or (ii) the absence of light (De Hullu and Gimingham, 1984) and the potential allelopathic effects on seed germination under the dense *Calluna* canopy in mature ones (Bonanomi et al., 2005), might impede seedling recruitment (Henning et al., 2017). Consequently, further assessments of the reproductive potential of *Calluna* plants subjected to different N inputs in these rear-edge heathlands are desirable, especially if prescribed burning for heathland rejuvenation or nutrient removal is to be applied (Måren et al., 2010; Valbuena et al., 2000).

Secondly, these results evidenced the importance of undertaking long-term studies and including multiple life-history stages when assessing the response of the *Calluna*-heathland ecosystem to global change, partially in accordance with Jones and Power (2015) and

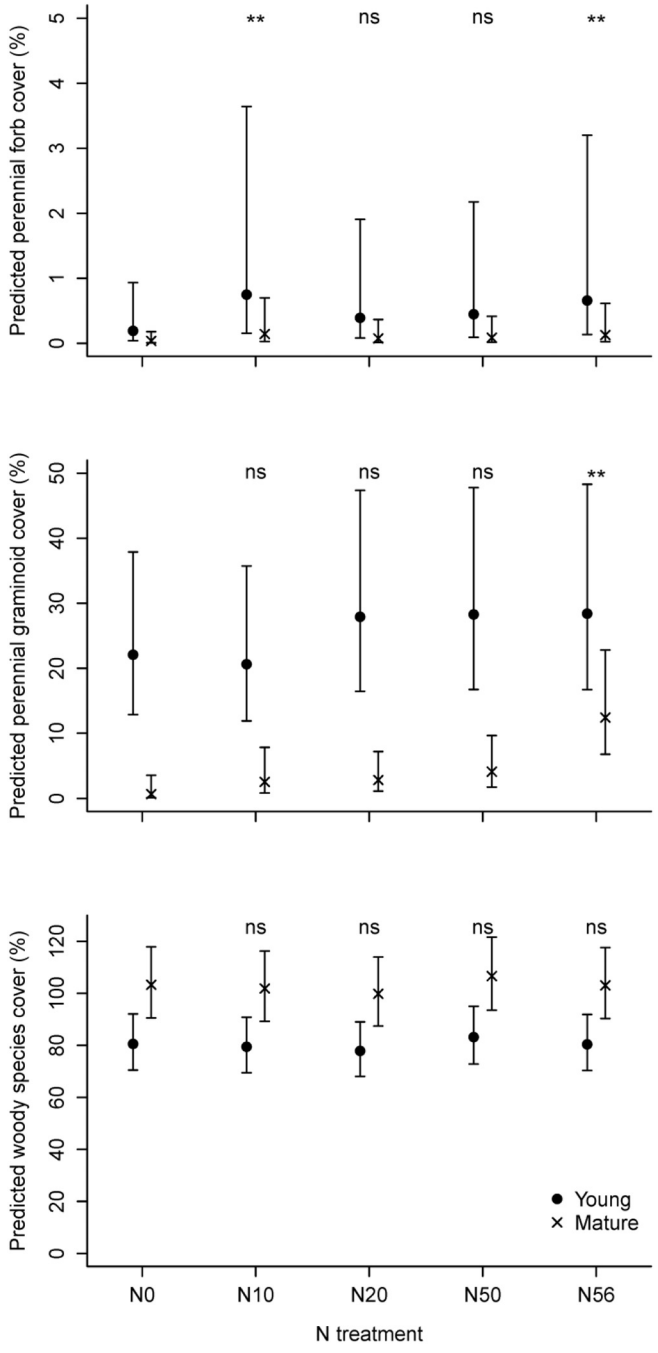

Fig. 2. Model predicted values (mean ± 95% confidence intervals) of the percentage cover (%) of perennial forbs, perennial graminoids, and woody species, in the two differently aged heathland areas [young (black filled circle), mature (cross)] and the five N treatments: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) for 1 year (short-term); and 56 kg N ha^{-1} yr^{-1} (N56) for 9 years (long-term). Significance levels of N treatments with respect to the control treatment (N0) are indicated by *** ($0.001 > p$), ** ($0.01 > p > 0.001$), * ($0.05 > p > 0.01$), and ns ($p > 0.05$).

Meyer-Grünefeldt et al. (2015, 2016). On the one hand, the *Calluna* plants of the surveyed montane heathlands with a short vegetation growing period during the lowest precipitation months (Calvo-Fernández et al., 2017) may rapidly uptake N and increase tissue N content right after N addition (Calvo-Fernández et al., 2018; "nutrient-conserving strategy" sensu Friedrich et al., 2011), but may require successive favourable growing seasons to attain noticeable N-induced changes in biomass accumulation (Calvo et al., 2002, 2005; see also Southon et al., 2012). This idea would explain the comparatively low growth rate and small size (height: mean ± standard deviation = 20.5 ± 7.1 cm; unpublished data) achieved by the young (9-year-old) *Calluna* plants recruited after prescribed burning at the experimental plots [percentage cover: mean ± standard deviation = 63.7 ± 12.2%, considerably lower than the 90% established by Gimingham, 1972 at the building phase (7–13 years old)]. As well as it would explain the fact that the slow-growing mature (>30-year-old) *Calluna* plants have not yet reached the degenerate phase [established by Gimingham, 1972 for *Calluna* individuals 16 to 29 or more years of age] and are, thus, still able to withstand competition with grasses (Aerts et al., 1990; Alonso and Hartley, 1998).

On the other hand, *Calluna* plant responses to cumulative high-N loads varied greatly with the plant's life-history stage at the studied rear-edge heathlands. Contrarily to mature *Calluna* plants (see Calvo-Fernández et al., 2015), young plants recovering slowly from management showed early signs of N saturation (sensu Aber et al., 1989) after 9 years of N fertilisation, with reduced annual growth and flowering despite of high N and phosphorous (P) foliar tissue contents (Calvo-Fernández et al., 2018). This finding would indicate that the long-term increased availability of N (i.e., cumulative dose of 504 kg N ha^{-1}) may have exceeded the plant's N demand and assimilation rate. This could be related to the low root development of these rear-edge *Calluna* plants in the early growth stages (Meyer-Grünefeldt et al., 2016) and to the increased competition for belowground resources with perennial graminoids at the experimentally-created bare soil patches (Hartley and Amos, 1999; Heil and Bruggink, 1987; Friedrich et al., 2011). It is most likely that the application of prescribed burning to rejuvenate the mature *Calluna*-heathland had created open spaces rapidly colonised by fast-growing graminoid species (like *Carex pilulifera*, *Festuca rubra*, *Juncus squarrosus*, and *Nardus stricta*, already present in the mature heathland) that outcompeted *Calluna* at the pioneer stage (see Barker et al., 2004; Hartley and Amos, 1999; Heil and Bruggink, 1987; Friedrich et al., 2011); resulting in high graminoid cover values at the building stage. This may have further implied less availability of light for young *Calluna* plants, a resource that might have limited *Calluna* plant productivity (Aerts et al., 1990), contributing to N saturation in this rear-edge heathland location (Aber et al., 1989).

4.2. Vegetation and functional group responses to cumulative high-N loading

Neither plant species composition nor species richness responded to the experimental addition of N in the studied rear-edge *Calluna*-heathlands, although major reductions in the percentage cover of non-vascular plant functional groups (i.e., bryophytes and lichens) were detected with cumulative (9-year) high-N (56 kg N ha^{-1} yr^{-1} plus background deposition) inputs at both young and mature life-cycle stages. Furthermore, we found low percentage cover values of annual/perennial forbs and annual graminoids at all N-fertilisation treatments and life-cycle stages, with high within plot variability especially in young heathlands. Perennial graminoids were rather abundant in young heathlands, but did not respond to the addition of N; in contrast with mature heathlands where they exhibited lower cover values and generally augmented with cumulative high-N loading.

It has been suggested that the lack of an N-driven effect on the heathland vegetation could be due to a prior loss of N-sensitive species in areas with historically high-N inputs (Emmett, 2007; Soons et al., 2017). However, no remarkable decline in the number of species inhabiting the studied rear-edge heathlands has been observed since the 1980s (Calvo et al., 2002, 2005, 2007, 2012; Cuesta et al., 2008). These results may, therefore, indicate that these heathlands are moderately resistant to increased N availability (up to 56 kg N ha^{-1} yr^{-1} plus background deposition) in terms of vascular vegetation structure and functional composition (see Calvo et al., 2005), and may require longer time periods (>10 years) for the negative impact of high-N availability to become evident (see Calvo-Fernández et al., 2018). In contrast,

Table 3
Plant species percentage cover (%) values (mean and standard error in parentheses) for each N treatment in young heathlands. N treatments: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) for 1 year (short-term); and 56 kg N ha^{-1} yr^{-1} (N56) for 9 years (long-term). Plant functional groups: AG = annual graminoid, PG = perennial graminoid, AF = annual forb, PF = perennial forb, W = woody species, B = bryophyte, and L = lichen.

		N treatment				
	Functional group	N0	N10	N20	N50	N56
Aira caryophyllea L.	AG	0.2 (0.1)	1.7 (0.8)	1.2 (0.7)	2.0 (1.5)	4.3 (1.7)
Agrostis capillaris L.	PG				0.2 (0.2)	
Bryophyta Schimp.	B	11.8 (3.3)	17.1 (4.8)	15.3 (1.9)	13.3 (2.4)	4.3 (1.7)
Calluna vulgaris (L.) Hull	W	63.8 (3.9)	63.9 (4.0)	67.5 (3.8)	61.9 (5.2)	61.3 (3.9)
Carex asturica Boissier	PG	0.5 (0.4)	2.1 (1.5)	1.2 (0.7)	0.4 (0.4)	
Carex nigra (L.) Reichard	PG	1.9 (1.7)	0.5 (0.4)	1.1 (1.0)	1.9 (1.2)	2.6 (1.7)
Carex pilulifera L.	PG	1.8 (1.0)	1.6 (0.8)	1.8 (1.0)	2.3 (1.5)	9.4 (4.4)
Cetraria islandica (L.) Ach.	L	7.8 (4.0)	2.4 (0.8)	4.5 (2.4)	7.8 (4.1)	0.1 (0.0)
Cladonia spp. P. Browne	L	4.8 (4.0)	0.2 (0.1)	1.1 (0.5)	4.4 (1.7)	<0.1 (0.0)
Conopodium majus (Gouan) Loret.	PF		0.1 (0.1)	0.3 (0.2)		
Cytisus oromediterraneus Rivas Mart. et al.	W	0.4 (0.4)	1.3 (1.1)	1.3 (1.3)	0.1 (0.1)	
Daboecia cantabrica (Huds.) Koch	W	0.1 (0.1)		0.1 (0.1)	0.2 (0.1)	
Deschampsia flexuosa (L.) Trin.	PG	2.0 (0.6)	2.6 (0.8)	2.8 (0.5)	2.3 (0.7)	1.5 (0.6)
Erica australis L.	W	1.8 (0.9)	0.9 (0.4)	0.4 (0.3)	5.2 (3.3)	2.6 (1.6)
Erica tetralix L.	W	6.4 (3.7)	1.9 (1.1)	3.1 (1.4)	11.6 (3.4)	11.3 (4.8)
Festuca rubra L.	PG	7.4 (1.4)	7.1 (2.0)	7.3 (2.9)	2.5 (1.1)	5.0 (1.9)
Galium saxatile L.	PF		0.1 (0.1)	0.1 (0.1)	<0.1 (0.0)	0.1 (0.1)
Hieracium pilosella L.	PF		0.2 (0.2)			
Jasione montana L.	AF					0.1 (0.1)
Juncus squarrosus L.	PG	2.6 (1.5)	2.8 (1.2)	4.2 (2.3)	11.4 (3.1)	6.2 (2.3)
Luzula spp. DC.	PG	0.1 (0.1)				
Nardus stricta L.	PG	6.5 (2.7)	3.3 (1.0)	9.1 (3.4)	7.2 (2.8)	3.9 (1.8)
Polygala vulgaris L.	PF	0.1 (0.1)	0.1 (0.1)	0.1 (0.0)		
Potentilla erecta (L.) Raeusch.	PF	0.1 (0.1)			1.3 (0.7)	0.5 (0.3)
Pterospartum tridentatum L.	W	0.1 (0.1)				
Rumex acetosella L.	PF	0.6 (0.4)	0.4 (0.3)	0.2 (0.1)	<0.1 (0.0)	0.6 (0.3)
Scilla spp. L.	PG					<0.1 (0.0)
Sedum album L.	PF		0.1 (0.1)	0.1 (0.1)		
Thymelaea dendrobium (Lam.) Endl.	PF	0.3 (0.3)	1.9 (0.8)	0.9 (0.7)		
Vaccinium myrtillus L.	W	9.0 (4.1)	6.6 (4.5)	11.1 (6.4)	7.9 (4.0)	1.5 (0.8)

north-western and central *Calluna*-heathlands most often experienced the loss of plant diversity (Britton and Fisher, 2007; Maskell et al., 2010; Southon et al., 2013; see meta-analysis by De Schrijver et al., 2011) and pronounced changes in plant species dominance (Aerts et al., 1990; Bobbink and Heil, 1993; Heil and Diemont, 1983; Prins et al., 1991) under elevated N loading, generally linked to an increased *Calluna* susceptibility to environmental stresses (e.g., herbivory, frost, and winter drought).

Table 4
Plant species percentage cover (%) values (mean and standard error in parentheses) for each N treatment in mature heathlands. N treatments: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) for 1 year (short-term); and 56 kg N ha^{-1} yr^{-1} (N56) for 9 years (long-term). Plant functional groups: AG = annual graminoid, PG = perennial graminoid, AF = annual forb, PF = perennial forb, W = woody species, B = bryophyte, and L = lichen.

		N treatment				
	Functional group	N0	N10	N20	N50	N56
Aira caryophyllea L.	AG	<0.1 (0.0)	<0.1 (0.0)			
Agrostis capillaris L.	PG					0.3 (0.2)
Bryophyta Schimp.	B	4.6 (1.8)	5.3 (1.6)	6.2 (1.8)	8.3 (3.4)	0.5 (0.2)
Calluna vulgaris (L.) Hull	W	81.9 (2.1)	78.3 (2.2)	78.1 (2.1)	79.8 (1.8)	81.7 (2.1)
Carex nigra (L.) Reichard	PG				0.4 (0.4)	<0.1 (0.1)
Carex pilulifera L.	PG	<0.1 (0.0)		<0.1 (0.0)		2.6 (0.9)
Cetraria islandica (L.) Ach.	L	11.0 (1.6)	10.4 (1.7)	13.3 (2.2)	13.8 (3.6)	2.0 (0.9)
Cladonia spp. P. Browne	L	7.5 (2.0)	9.3 (1.6)	11.6 (1.6)	11.5 (2.2)	0.2 (0.1)
Conopodium majus (Gouan) Loret.	PF	0.1 (0.1)	0.1 (0.0)			
Cytisus oromediterraneus Rivas Mart. et al.	W	0.1 (0.1)		0.1 (0.1)	<0.1 (0.0)	
Daboecia cantabrica (Huds.) Koch	W					
Deschampsia flexuosa (L.) Trin.	PG	<0.1 (0.0)	0.1 (0.1)	0.3 (0.1)	0.3 (0.2)	
Erica australis L.	W		0.3 (0.3)	0.3 (0.3)	0.8 (0.6)	
Erica tetralix L.	W	10.7 (5.2)	16.8 (8.3)	7.0 (3.6)	13.8 (7.7)	
Festuca rubra L.	PG	0.4 (0.2)	1.1 (0.9)	1.4 (0.3)	1.4 (0.6)	
Galium saxatile L.	PF		0.1 (0.1)	0.1 (0.1)	0.5 (0.5)	
Jasione montana L.	AF			0.1 (0.1)	0.2 (0.1)	
Juncus squarrosus L.	PG	<0.1 (0.0)		0.6 (0.4)	0.1 (0.1)	
Luzula spp. DC.	PG			0.1 (0.1)		
Nardus stricta L.	PG	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)	0.9 (0.7)	
Polygala vulgaris L.	PF		<0.1 (0.0)	<0.1 (0.0)	0.1 (0.1)	
Potentilla erecta (L.) Raeusch.	PF					
Rumex acetosella L.	PF					
Thymelaea dendrobium (Lam.) Endl.	PF		0.4 (0.4)	0.6 (0.6)	0.6 (0.5)	
Vaccinium myrtillus L.	W	10.3 (5.1)	12.5 (5.9)	9.6 (4.5)	9.4 (4.8)	

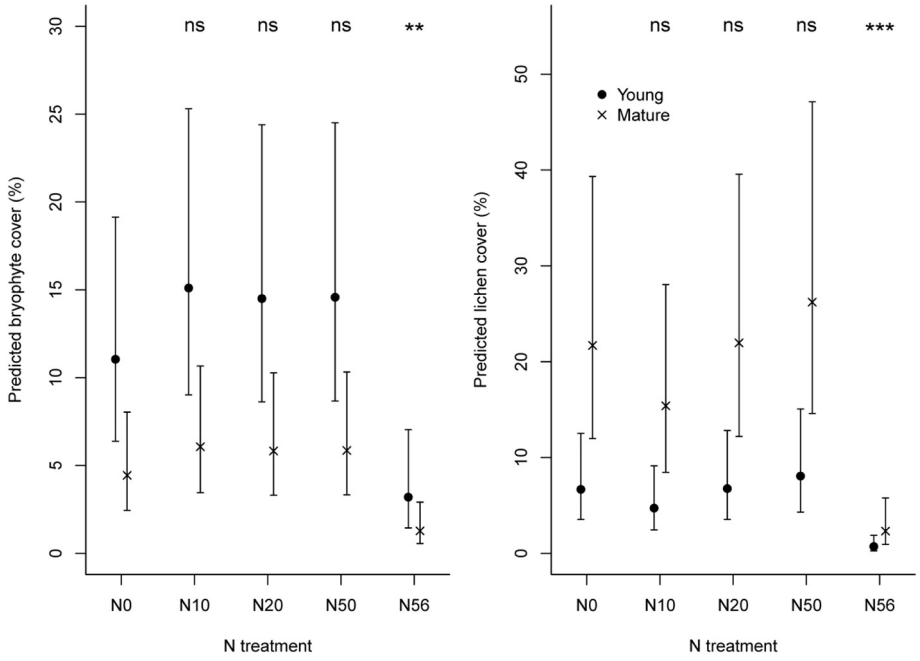

Fig. 3. Model predicted values (mean ± 95% confidence intervals) of the percentage cover (%) of bryophytes and lichens in the two differently aged heathland areas [young (black filled circle), mature (cross)] and the five N treatments: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) for 1 year (short-term); and 56 kg N ha^{-1} yr^{-1} (N56) for 9 years (long-term). Significance levels of N treatments with respect to the control treatment (N0) are indicated by *** ($0.001 > p$), ** ($0.01 > p > 0.001$), * ($0.05 > p > 0.01$), and ns ($p > 0.05$).

The observed negative responses of bryophytes and lichens to cumulative (9-year) high-N (56 kg N ha^{-1} yr^{-1} plus background N deposition) loading in our rear-edge *Calluna*-heathlands are consistent with many previous studies from north-western and central European heathlands (e.g., Bähring et al., 2017; Caporn et al., 2014; Southon et al., 2013). In these heathlands non-vascular species reacted faster and more sensitive than vascular plants to increased N deposition (e.g., 2 years, 5 kg N ha^{-1} yr^{-1}: Bähring et al., 2017; 4 years, 10 kg N ha^{-1} yr^{-1}: Britton and Fisher, 2007; 4 years, 10 kg N ha^{-1} yr^{-1}: Pilkington et al., 2007). Contrarily to these studies, however, we only found significant reductions in the percentage cover of both cryptogam functional groups after many years of N fertilisation and under high-N inputs (i.e., cumulative dose of 504 kg N ha^{-1}; see De Schrijver et al., 2011). This likely indicates that the rate of change due to

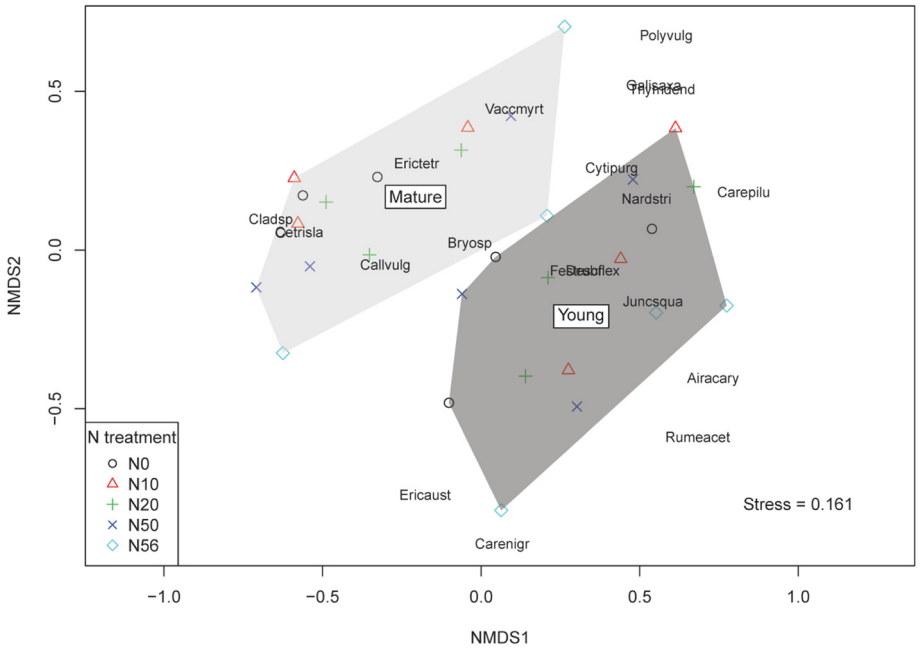

Fig. 4. Plant species composition of the two heathland ages [young (dark grey), mature (light grey)] and the five N treatments represented by the first two axes of the NMDS ordination. N treatments: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) for 1 year (short-term); and 56 kg N ha^{-1} yr^{-1} (N56) for 9 years (long-term). Plant species names are a combination of 4 (genus name) by 4 (species name) letters. See Tables 3 and 4 for full species names. Permutational MANOVA revealed significant differences in species composition between the two heathland ages (see Table 5).

Table 5
Results of the permutational MANOVA testing for differences in plant species composition among the two heathland ages (young, mature) and the five N treatments: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) for 1 year (short-term); and 56 kg N ha^{-1} yr^{-1} (N56) for 9 years (long-term). Df = degrees of freedom. Significant *p*-values are in bold face.

Factor	Df	Sum of squares	F value	*p* value
Age	1	0.48	8.67	**0.001**
N treatment	4	0.17	0.78	0.698
Age:N treatment	4	0.06	0.28	0.995
Residual	20	1.11		

enhanced N availability in the percentage cover of non-vascular vegetation of rear-edge *Calluna*-heathlands is slow and/or requires greater doses of N deposition in comparison to north-western and central heathlands. This again suggests that *Calluna*-heathlands at their southern-most distribution limit are relatively more resistant to or cope better with increased N availability also regarding non-vascular vegetation structure.

Alternatively, the absence of broad N-driven responses of vascular and non-vascular plants to enhanced N-availability could be the result of either an effect of the experimental design (i.e., 2 m × 2 m plot-based field experiment with considerable variation among plots), an effect of the short-term (1-year) duration of the N-fertilisation treatments (N10, N20, and N50), or both. However, this might not be the case, as prior N-addition plot-based experiments at these rear-edge montane heathlands detected significant changes in vascular plant species richness and percentage cover over the short-term (i.e., 1 m × 1 m experimental plots, 3 months to 2 years; Calvo et al., 2005, 2007; Cuesta et al., 2008). Similarly, previous N-fertilisation plot-based experiments in *Calluna*-heathlands (e.g., Bähring et al., 2017; Britton and Fisher, 2007; Pilkington et al., 2007) and grassland ecosystems (e.g., Clark and Tilman, 2008; Reich, 2009; Van den Berg et al., 2011) reported

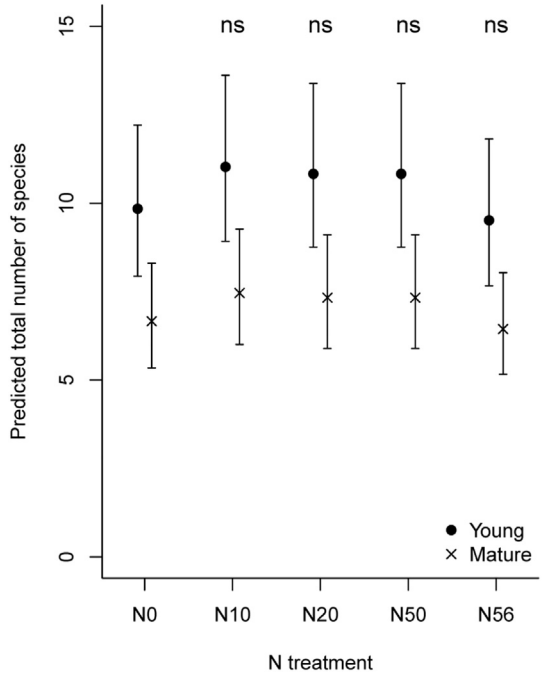

Fig. 5. Model predicted values (mean ± 95% confidence intervals) of plant species richness in the two differently aged heathland areas [young (black filled circle), mature (cross)] and the five N treatments: 0 kg N ha^{-1} yr^{-1} (N0; control), 10 kg N ha^{-1} yr^{-1} (N10), 20 kg N ha^{-1} yr^{-1} (N20), and 50 kg N ha^{-1} yr^{-1} (N50) for 1 year (short-term); and 56 kg N ha^{-1} yr^{-1} (N56) for 9 years (long-term). Significance levels of N treatments with respect to the control treatment (N0) are indicated by *** ($0.001 > p$), ** ($0.01 > p > 0.001$), * ($0.05 > p > 0.01$), and ns ($p > 0.05$).

significant effects of increased N loading on plant species richness, composition and/or functional groups over different time scales.

4.3. Implications for heathland management at the rear-edge of the ecosystem's distribution

Similarly to most *Calluna*-heathlands across Europe (Webb, 1998), the studied rear-edge heathlands have historically been maintained by frequent small-scale perturbations, mainly controlled burning and cutting to create pastureland for breeding livestock. In the last few decades, the decline or cessation of these practices has led to the senescence of *Calluna* plants which might eventually reach a degenerate stage and lose their ability to outcompete grasses and encroached trees/shrubs (*Betula pubescens* Ehrh., *Pinus sylvestris* L., and *Cytisus oromediterraneus* Rivas Mart. et al.); as happened in other north-western, central and southern heathlands (e.g., Bartolomé et al., 2005; Rose et al., 2000). Prior experimental studies comparing different management alternatives in the surveyed rear-edge heathlands supported repeated burning on a 15–20-year rotation to prevent the degenerate phase from occurring (Calvo et al., 2002, 2012). However, our findings further suggest that rejuvenation by prescribed burning alone may be ineffective to preserve these heathlands under elevated airborne N deposition, as fire promoted invasion by graminoid species in our experimental plots at the pioneer phase (see Barker et al., 2004; Friedrich et al., 2011; Hartley and Amos, 1999; Heil and Bruggink, 1987). It would be therefore necessary to complement regular (>30-year; see Velle et al., 2012) burning with livestock grazing at moderately-low stocking rates (Pakeman et al., 2003) before the building stage is attained (i.e., <5 years after fire; Gimingham, 1972), allowing *Calluna* to outcompete graminoids for light (Alonso and Hartley, 1998). Nonetheless, the most suitable fire and grazing intensities, frequencies and extents to minimise the impact of N accumulation should be determined by future research, especially regarding the most sensitive species (i.e., bryophytes and lichens).

5. Conclusions

To our knowledge, this is the first study revealing that *Calluna*-heathlands at the low-latitude distribution limit are fairly resistant to cumulative (9-year) high-N (56 kg N ha^{-1} yr^{-1} plus background deposition) inputs, at both the building/young and mature growth stages, regarding plant functional groups relative abundances, species composition and richness. The general lack of N-driven responses of the studied rear-edge heathlands to the long-term experimental addition of N diverges within the ecosystem's distribution range, as north-western and central European heathlands are broadly very sensitive to enhanced N availability. Furthermore, we reported (1) dose-related responses of *Calluna* annual growth and flowering to the addition of N (1 year; 10, 20, and 50 kg N ha^{-1} yr^{-1}); (2) early signs of N saturation of young *Calluna* plants; and (3) a marked reduction in the percentage cover of bryophytes and lichens only with very high doses of N (i.e., cumulative dose of 504 kg N ha^{-1}). These results potentially indicate that rear-edge montane heathlands may be of vital importance to unravel the mechanisms of heathland ecosystem resilience (Meyer-Grünefeldt et al., 2016) under the uncertainty of global changes in the upcoming decades (N fertilisation effects vs. warming and drought effects; Peñuelas et al., 2017).

Acknowledgements

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